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Interpreting Botanical Progress

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E. H. FULLING

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Bacterium. All bacterial plant pathogens would thus be included in the genus *Bacterium*. Lehmann and Neumann's system has been followed more by European than by American pathologists. In the earlier years, Smith followed Migula's classification. In 1905 (24) he suggested changes in Migula's system, proposing a new genus, *Aplanobacter*, for non-motile rods and using *Bacterium* for polar flagellate organisms and *Bacillus* for peritrichous rods. Some plant pathologists have followed one of these systems and others another. Although the number of genera involved in all three systems is not large, use of the same generic term for different characteristics in the different systems has led to a great deal of confusion. In

COMPARISON OF SYSTEMS

Author	Non-motile	Motile with polar flagella	Motile with peritrichous flagella	Spore-formers	Non-spore-formers
Migula (1894 & 1900)	*Bacterium*	*Pseudomonas*	*Bacillus*		
Lehmann & Neumann (1896 & 1927)				*Bacillus*	*Bacterium*
Smith (1905)	*Aplanobacter*	*Bacterium*	*Bacillus*		
Bergey (1923 to 1939)		*Phytomonas*	*Erwinia*		

naming an organism it has been necessary to state which system has been followed, and many have found it advisable to include in footnotes the synonyms in other systems. An organism named *Bacterium campestre* would be followed in a footnote with the binomials in other systems, *Pseudomonas campestris, Phytomonas campestris*. Such confusion is due partly to the use of different systems of classification but primarily to our lack of knowledge of the organisms themselves. Just as the above systems were based on the single character of motility or spore formation, the two genera, *Phytomonas* and *Erwinia*, in Bergey's system (1) were at first separated from all other bacterial organisms on the basis of plant pathogenicity. Non-motile and polar flagellate organisms were combined in the genus *Phytomonas* and peritrichous organisms put in the genus *Erwinia*. On the whole, however, Bergey's system

of classification is based on physiological as well as morphological characters.

With our increasing knowledge of the cultural, physiological and other characteristics of bacteria, it has been pointed out (5, 6, 11, 21) that the use of any one character to limit genera, whether it be motility, pathogenicity or any other character, is no longer justified and does not lead to the arrangement of bacteria in natural groups of related organisms. Motile and non-motile strains occur in many groups of bacteria. There are motile and non-motile strains of the crown-gall organism, *Bacterium tumefaciens*. Pathogenic organisms often lose their pathogenicity. They are not always associated with their host plants, sometimes being isolated from soil.

In recent systems of classification the use of a number of characters has supplanted the use of any one characteristic, and search for new differential media and new tests to differentiate bacteria continues. Use of physiological characters in defining genera of bacteria was first suggested more than 40 years ago (16). In 1908 and 1909, Orla-Jensen (19), for the first time, based his classification mainly on physiological characters. Kluyver and van Niel (15) maintained that while morphology still remains the first and most reliable guide to the natural relationships of different bacterial groups, "nowadays the indispensability of physiological characters for classification has been generally accepted, which is only natural as these physiological differences must be considered as expressions of variations in submicroscopical morphology". As far back as 1914 (27) Winslow stated that "there is no fundamental distinction between morphological and physiological properties, since all are at bottom due to chemical differences in germ plasm, whether they happen to manifest themselves in the size and arrangement of parts or in the ability to utilize a certain foodstuff. Indeed biochemical properties have a peculiar and unique significance among the bacteria since it is precisely along the lines of metabolism that these organisms have obtained their most remarkable differentiation. The higher plants and animals have developed complex structural modifications to enable them to obtain food materials of certain limited kinds. On the other hand, the bacteria have maintained themselves by acquiring the power of assimilating simple and abundant foods of varied sorts. Evolution has developed gross structure in one case without altering metabolism; it has produced

a diverse metabolism in the other case without altering gross structure. There is as wide a difference in metabolism between the pneumococci and the nitrifying bacteria as there is in structure between a liverwort and an oak".

Dissatisfaction with the earlier systems of classification has led to study of the morphological and physiological characters and the staining reactions of plant pathogens. To begin with, comparisons have been made of the published descriptions of these bacteria and natural groups pointed out by Rahn (20), Burkholder (5, 6) and others. They have indicated that bacterial plant pathogens with peritrichous flagella in the genus *Erwinia,* relatively few in number, form a fairly well defined natural group, very similar to *Escherichia coli* (Migula) Castellani and Chalmers. On the other hand, the polar flagellate and non-motile organisms in Bergey's genus *Phytomonas* include by far the larger number of plant parasites and are a heterogeneous mixture which can be divided into smaller groups of related organisms. In 1930 Burkholder (5) showed that there are three or possibly four such natural groups in the genus *Phytomonas:* a yellow group of organisms including *Bacterium campestre,* a fairly well defined green fluorescent group, and a *stewarti* group of non-motile Gram-positive organisms, each of which, except for pathogenicity, might find a place in genera of Bergey's Family Bacteriaceae. In 1937 Rahn (22) outlined a natural system of classification, emphasizing physiological as well as morphological characters. He proposed a new family, *Enterobacteriaceae,* for Gram-negative rods, non-motile or peritrichous, and included in this family *Escherichia* and *Erwinia* but did not name any species. In his family *Pseudomonadaceae,* for Gram-negative rods motile by polar flagella, he includes the genus *Pseudomonas,* Bergey's green fluorescent species and 77 of the 84 species in *Phytomonas.*

When the last (fifth) edition of Bergey's Manual was published (1), Burkholder (6) reclassified the bacterial plant pathogens. He did not change either of the two generic names, *Erwinia* or *Phytomonas,* but indicated that eventually new generic names would have to be proposed. Plant pathogens, he stated, were no longer to be considered a distinct group by themselves, and in his rearrangement he attempted to show the natural relationships of *Erwinia* and of the various groups of *Phytomonas* in the order Eubacteriales. He re-

moved these two genera from the family Bactereaceae and placed them in two different families, *Erwinia* in Enterobacteriaceae with *Escherichea coli* and *Aerobacter,* as Rahn had done (22), and *Phytomonas* in the family Pseudomonadaceae next to *Pseudomonas.* The type species of what he calls *Phytomonas* proper is *Phy. campestris;* and included in this group are other yellow organisms such as *Phy. phaseoli, Phy. juglandis, Phy. malvacearum, Phy. translucens.* Here he lists 41 species. The remainder of the 137 *Phytomonas* species are listed in two appendices. In Appendix I are 74 species that Burkholder says cannot be distinguished from species included in *Pseudomonas,* except for plant pathogenicity. Many of them produce green fluorescent pigment. In Appendix II are 22 species of *Phytomonas* that he says cannot be distinguished from species included in Rhizobiaceae, except for plant pathogenicity. They are the plant pathogens that produce galls, wilts, *etc.* Both Gram-negative and Gram-positive organisms are included in this group. Poorly described organisms and those whose pathogenicity has not been proved are grouped together in a third appendix. "Wherever a complete description is given of a pathogen, the species fits very readily into one of the three groups of *Phytomonas* or into the genus *Erwinia*".

The ideal way to compare and classify the plant pathogens would be to study them all together at one time on the same media and under the same conditions, but this is a practical impossibility. Interest in and discussion of systems of classifications have, however, done much to stimulate comparative cultural and biochemical studies of smaller groups of such organisms, some emphasizing one kind of test and some another. Probably the green fluorescent group has received more attention than the other groups included under *Phytomonas.* Clara, in 1934 (8) compared 19 of the green fluorescent plant pathogens and *Pseudomonas fluorescens.* He found them a closely related group with *Ps. fluorescens* apparently "a border-line form linking the close relationship of the green-fluorescent plant pathogens to the green-fluorescent non-phytopathogenic forms".

In an article published in 1939, Dowson (11) gives the results of a detailed study of the cultural and biochemical characters of a large number of Gram-negative bacterial plant pathogens that he compared on a variety of media with *Bacterium coli,* used in the

sense of Lehmann and Neumann, and *Ps. fluorescens*. He concluded that the plant pathogens could be arranged in three distinct groups, one like *Bact. coli* producing acid or acid and gas in salicin, a second group like *Ps. fluorescens* which produced no acid in lactose, maltose and salicin, but produced fluorescence on some media. The third group did not produce acid or gas in salicin and produced an abundant slimy yellow growth on solid media. The last two groups are similar to those mentioned by Burkholder in 1930 (5). To the first group Dowson gave the genus name *Bacterium* L. & N. (*e.g., Bacterium carotovorum*), to the second the genus name *Pseudomonas* Migula Emended (*e.g., Ps. syringae*). For the third and yellow group he proposed a new name, *Xanthomonas,* with *X. hyacinthi* as the type species. He thus definitely transfers some of the plant pathogens from *Phytomonas* to *Pseudomonas, i.e.,* the green fluorescent organisms, and to his new genus *Xanthomonas,* the yellow organisms. He also emphasizes the importance of the Gram stain which he says "reveals such a fundamental difference in the constitution of the proteins of the two groups that they are probably not closely related". He excludes the genera *Bacterium* Migula, *Aplanabacter* Smith, *Erwinia* and *Phytomonas* as unjustified because they were created on one character alone, motility or pathogenicity, and because *Phytomonas* is a homonym. Dowson has, then, three groups, the soft rot group represented by *Bacterium carotovorum,* the green fluorescent group with *Pseudomonas syringae,* and the yellow group with *Xanthomonas hyacinthi.*

In 1942 Starr and Burkholder (25) reported the results of comparative studies of groups of bacterial plant pathogens in relation to their ability to produce lipolytic enzymes and so to split fats. Here they change the names of some of the natural groups in *Phytomonas* to indicate their relationship to other genera. These are the same natural groups pointed out earlier by Burkholder, Dowson and others, and which, presumably, will be included in any new editions of Bergey, if Burkholder continues to edit the material on plant pathogens. These are, therefore, of particular interest. They found that the different physiological groups of *Phytomonas, i.e.,* the yellow group, the green fluorescent group, *etc.,* varied in their ability to decompose cotton seed oil and that members of any one of the groups usually have a "similar and characteristic reaction".

They emphasized the possible value of this lipolytic activity of bacteria as a taxonomic character. For the yellow group, with *Phytomonas campestris* as the type species, which formerly was called *Phytomonas* proper (1), Starr and Burkholder use Dowson's (11) new genus *Xanthomonas*. Thus we have 24 species and varieties changed from *Phytomonas* to *Xanthomonas* with *X. campestris* as the type species. These include such familiar organisms as *X. malvalcearum, X. phaseoli, X. pruni* and *X. vasculorum*. Twenty-one of the twenty-four decompose cotton seed oil, the fat used in this experiment. One of the three species in this group, which is not lipolytic, *X. rubrilineans,* they say does not conform closely in other cultural characters. The green fluorescent group Burkholder still called *Phytomonas* in the fifth edition of Bergey but put it in Appendix I as indistinguishable from *Pseudomonas,* except for pathogenicity. Twenty-seven of these Starr and Burkholder (25) changed from *Phytomonas* to *Pseudomonas,* including *Ps. syringae* and *Ps. delphinii*. Starr and Burkholder found that the majority of plant pathogens in this group did not decompose cotton seed oil, although some of the saprophytic species, including *Ps. fluorescens,* were strongly lipolytic. Four species were lipolytic but possibly three of them did not belong in this group.

The gall-forming group, which Burkholder placed in Appendix II of Bergey's 5th edition as closely related to species of *Rhizobium* or related genera, Starr and Burkholder did not change, although it showed no typical lipolytic reaction, and six strains of three genera of the Rhizobiaceae also did not split fats. These gall-producers they still call *Phytomonas tumefaciens, Phy. savastanoi, etc.*

Other important changes in the classification of bacterial plant pathogens have appeared in the literature. Conn, Wolfe and Ford (10) in 1940 reported that *Phytomonas tumefaciens* is so nearly like *Rhizobium* that it is very difficult to tell them apart by cultural tests. They tested eight gall- and wilt-producing species and concluded that *Phy. rhizogenes,* the hairy root organism, and *Phy. tumefaciens* are very closely related to species in the genera *Rhizobium* and *Alcaligenes*. They believe there is little doubt that *Phy. rhizogenes* and *Phy. tumefaciens* belong in the family Rhizobiaceae.

In 1942 Conn (9) proposed the new genus *Agrobacterium* with *A. tumefaciens* as the type species, and gave a description of the

genus. Speaking of *Alcaligenes radiobacter,* he says it is "very similar to the legume nodule organisms, *Rhizobium* spp. and to the bacteria causing crown gall and hairy root (now in *Phytomonas*). Students of these groups are coming to think that all these species should be close together in the classification. The legume nodule organisms undoubtedly constitute a definite and easily recognized genus; but after consultation with bacteriologists who have studied both the genus *Rhizobium* and the closely related plant pathogens, it seems that a new genus is called for. This genus should contain the plant pathogens closely related to the crown gall organisms, the soil species now in *Alcaligenes* and other saprophytic organisms that may be found to be similar in morphology and physiology. For this new genus the name *Agrobacterium* is now proposed with *A. tumefaciens* as its type species. Placed with this should be *Agrobacterium radiobacter* and *Agrobacterium rhizogenes* (syn. *Phytomonas rhizogenes*), the cause of hairy root". He leaves it for the phytopathologists to make the new combinations in this genus of related organisms listed in Appendix II of *Phytomonas* in the 5th edition of Bergey's Manual.

While most plant pathogens are Gram-negative, a few have been shown to be Gram-positive (12, 14, 23, 25). As a result, these organisms are now in the genus *Corynebacterium.* The type species is *C. diphtheriae,* the diphtheria organism. These organisms are aerobic, non-motile, Gram-positive, tend to form club-shaped cells, sometimes branched, and often have irregular bar or belt staining, among other characteristics. Jensen considered that *Corynebacterium insidiosum* and *C. michiganense* belong here, and also probably *Bacterium sepedonicum* and *Aplanobacter rathayi.*

Dowson recommends that the names of the Gram-positive bacteria be:

Corynebacterium sepedonicum (Spieckermann) N. comb.
C. rathayi (Smith) N. comb.
C. michiganense (Smith) Jensen
C. insidiosum (McCulloch) "
C. flaccumfaciens (Hedges) N. comb.
C. fascians (Tilford) N. comb.

Starr and Burkholder (24) make the following changes from *Phytomonas:*

Corynebacterium fascians
C. flaccumfaciens

C. insidiosum
C. michiganensis

These four organisms show slight or no fat-splitting ability.

In 1942 Skaptason and Burkholder (23) reported having made a thorough study of the morphology and physiology of the ring-rot pathogen, that it has all the characteristics of the genus *Corynebacterium,* and propose that the name be changed to *Corynebacterium sepedonicum* (Spieckermann *et* Kotthof) *comb. nov.*

Regarding the genus *Bacterium,* in 1918, Breed, Conn and Baker (3) suggested "that a temporary group be recognized to include species of non-spore-forming rods whose relationship to other species is obscure". In 1936 Breed and Conn (2) made this suggestion into a definite recommendation "that *Bacterium* be accepted as a temporary generic term with an admittedly unrecognizable type species, *Bacterium triloculare* Ehrenberg, to include those species of non-spore-forming, rod-shaped, motile or non-motile bacteria whose relationships to other bacteria are not clear. When relationships to other similar species have been developed by investigation, then this generic term would naturally be dropped". Accordingly, Bergey *et al.* (1) include in the family Bacteriaceae "a heterogeneous collection of genera whose relationships to each other and to other groups are not clear". In this family are ten genera including *Bacterium.* In *Bacterium* are miscellaneous species which, so far, cannot be classified.

In Appendix III of Bergey's 5th edition are listed organisms imperfectly described and some the pathogenicity of which has not been proved. It would seem that these organisms and the few remaining species of *Phytomonas,* such as *Phytomonas tardicrescens, Phy. stewarti, etc.,* whose relationship to other organisms is uncertain, might, for the present, all be placed in the genus *Bacterium* in the family Bacteriaceae provided for such organisms.

Regarding *Bacillus,* Winslow *et al.,* in their preliminary and final reports (28, 29), included spore-bearing rods. In 1935 Breed and St. John-Brooks (4) reported that the nomenclature committee of the International Society for Microbiology recommended that the term *Bacillus* be used as a generic name and "be so defined as to exclude bacterial species which do not produce endospores". This recommendation was approved by the Second International Microbiological Congress in London in 1936. The genus *Bacillus* is,

thus, no longer available for plant pathogens, and the genus *Bacterium* is available only temporarily, if we follow Bergey's classification for species whose relationship to other organisms in this system is uncertain. The term *Bacterium campestre* may be used but it would indicate that the relationship of this organism to other plant pathogens is uncertain.

Regarding *Aplanobacter,* Smith (24) states: "Under *Aplanobacter* I include all non-motile forms morphologically similar to the anthrax organism (*Bacillus anthracis* Cohn) the latter, however, being taken as the type of the genus". "For the present non-sporiferous forms resembling *Aplanobacter anthracis* are also included under this genus, but if it shall be decided, later on, that the difference between sporiferous and non-sporiferous forms is of generic significance, then the latter may be excluded". This appears to exclude our non-spore-forming plant pathogens.

Little need be said about the soft rot organisms. It is generally recognized that they are closely related to *Escherichia coli,* and in the 5th edition of Bergey's Manual the genus *Erwinia* is placed in the same family with this organism. Comparative studies (11, 13, 21, 26) continue to point out the close relation to coliform bacteria, but these soft rot organisms have not been placed in any other genus. They remain *Erwinia carotovora, etc.*

On the basis of Bergey's Manual and the changes indicated in the preceding discussions, the abbreviated list on page 665, indicates the present taxonomic status of bacterial plant pathogens.

Gall-producing organisms have been placed in the family Rhizobiaceae in a new genus *Agrobacterium,* and green fluorescent organisms, such as *Ps. syringae,* in *Pseudomonas.*

The relationship of a few of the Gram-negative wilt organisms is still uncertain and they have been retained in the genus *Phytomonas,* but as suggested above might better be placed in the temporary genus *Bacterium* provided for species which so far cannot be classified.

The yellow group of plant pathogens now are called *Xanthomonas* sp.; the soft rot organisms, *Erwinia carotovora, etc.,* are in the family *Enterobacteriaceae;* and Gram-positive organisms are in a separate order in the genus *Corynebacterium.*

Our bacterial plant pathogens are finding their places among related groups of bacteria. As further research deepens our insight

into the characteristics of plant pathogens, other changes in their taxonomy undoubtedly will be made.

CLASS—SCHIZOMYCETES
- Order I—Eubacteriales
  - Family II Rhizobiaceae
    - Genus I *Rhizobium*
    - Genus II *Chromobacterium*
    - Genus III *Alcaligenes*
    - Genus IV *Agrobacterium tumefaciens nov. gen.*
      Agrobacterium rhizogenes nov. gen.
  - Family III Pseudomonadaceae
    - Genus V *Pseudomonas*
      - " *syringae*
      - " *delphinii*
      - " *lachrymans*
      - " *pisi*
      - " *tabaci*
      - " *savastanoi*
    - Genus VI *Phytomonas*
      - " *stewarti*
      - " *manihotis*
      - " *tardicrescens*
      - Appendix II " *pseudotsugae*
      - " *gypsophilae*
    - Genus *Xanthomonas*
      - " *campestris*
      - " *phaseoli*
      - " *malvacearum*
      - " *juglandis*
  - Family X Enterobacteriaceae
    - Tribe I *Escherichieae*
      - Genus I *Escherichia coli*
    - Tribe II *Erwineae*
      - Genus I *Erwinia carotovora*
  - Family XI Bacteriaceae
    - Genus X *Bacterium*
  - Family XII Bacillaceae
    - Genus I *Bacillus*
- Order II—Actinomycetales
  - Family I Mycobacteriaceae
    - Genus I *Corynebacterium*
      - " *michiganense*
      - " *sepedonicum*
      - " *flaccumfaciens*
      - " *fascians*
      - " *insidiosum*
      - " *rathayi*

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PHYTOGEOGRAPHY OF PATAGONIA

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Patagonia is a region of low rainfall in southern Argentina which is occupied by a natural zone of xerophytic vegetation. Its name was given first to the Indians of the region by Magellan (41) and gradually through usage by the Spanish became associated with the territory (44). Its northern limit is the least sharply defined and occurs in the drainage areas of the Rios Negro and Colorado or between 41° and 43° S. Here the flora grades into the semi-xerophytic "bosques xerofiles" or "monte" and the pampas. To the east lies the Atlantic Ocean and to the west the "bosques subantarcticos", often spoken of as the Magellanic flora.

This is essentially the same delimitation as recognized by Ball (2, 3), but it does not agree with that of Blake and Atwood (8) whose usage is not in line with that of current plant geographers. The term "Western Patagonia" has often been used for parts of southern Chile bordering on Patagonia proper (35). The southern limit of Patagonia does not quite follow the Chilean-Argentine border nor does it include any of Tierra del Fuego or the Falkland Islands (Islas Malvinas). The rainfall of Patagonia is very light as compared with that along the Straits of Magellan. The xerophytic influence on the vegetation extends just below the Rio Gallegos. Tierra del Fuego and the Falkland Islands have none of the characters of a desert, nor may most of the plants be termed xerophytic.

The great Basin region of western North America presents in many respects a close approach in general appearance to Patagonia. The extent of the northern border is about equal to the distance from Mt. Shasta in northern California to the Great Salt Lake in Utah and lies at about the same distance from the equator. Were Patagonia placed on this line and pointed northward it would taper triangular fashion to a point in Canada in line with the northern end of Vancouver Island or the southern end of James Bay. In overall aspect the vegetation resembles that of the broad sparsely covered floors of the Great Basin. Comparison is found in the predominance of shrubs over a sparse herbaceous layer to the exclu-

sion of native trees. In comparative poverty of the flora, too, Patagonia is about equal to the Great Basin.

As to physical features both are bordered on the west by high mountains but otherwise are quite different. Only a few hills rise to insignificant heights out of the general flatness of Patagonia. The whole area is under 2,000 feet in elevation and slopes gently from the west to the east. The area is composed of terraced plains cut by swiftly running streams which rise in large glacial lakes. These rivers, all with few tributaries, are here mentioned in order as they occur from north to south: (*a*) the Rio Negro arises in Lago Nahuel Huapi and, together with (*b*) Rios Chubut and (*c*) Senger, drains northern Patagonia. With parallel courses in middle Patagonia are (*d*) Rio Deseado arising in Lago Buenos Aires, (*e*) Rio Chalia arising in Lago San Martin, and (*f*) Rio Santa Cruz arising in Lago Argentine. Finally the (*g*) Rio Coy and (*h*) Rio Gallegos drain southern Patagonia. Although they have practically no distinctive aquatic plants along their banks they have had a profound effect on the flora, for not only have they destroyed the flora through periodic inundations but they have replenished it by acting as migration lanes for a rich Andean flora. They serve as the water source for a limited amount of irrigated agriculture.

As suggested above, most Patagonian lakes are on the western border. Only three or four are in central Patagonia and are high in salt content. Frequent whitened circles mark the salt-encrusted basins of dry lakes. Geologically the area is extremely diverse. The swiftly running streams, often cutting deep courses, attest to the youthfulness of the terrain. Many localities near the coast are dominated by Tertiary sea deposits; in parts of the interior are recently extruded lavas standing in bold relief on the sedimentary layers. Occasionally in southern Patagonia evidences of glaciation are found. In general the surface layers show little relationship to the underlying foundation rock (44).

The climate is characterized by dryness and the prevailing southwesterly winds (52). These are a result of neighboring geographical features, including the combined influence of the Andes mountain chain and the Pacific Ocean. The winds are so constant that the dry leaves of perennial grass tussocks all point in one direction. In winter lost travellers scrape away the snow and from them find

their way. The rainfall is everywhere below 20 inches a year and over a considerable area below 10 inches. Here the rainfall contrast between the eastern and western slopes of the Andes is as marked as that between Puget Sound and eastern Washington.

The history of the Patagonian formations is closely related to that of the bordering Cordillera. Part of the area has probably been elevated since the Permian, first as the land mass now called Amazonia (1) and later in geologic time as Gondwana (45). There are land floras in both Cretaceous and Tertiary deposits, and the elements in these floras are related to both the subtropical floras found northward as indicated by an abundance of Gamopetalae (Apocynaceae, Bignoniaceae, Rubiaceae) and the Magellanic flora to the west as indicated by *Fitzroya* and other coniferous elements (7, 25). They do not have any particular bearing on the flora as it exists today, since none of the present day elements is represented in the fossil floras. Berry (7) says: "as the final uplift of the Andes, which is the main reason for the dissimilar climates and consequently dissimilar floras on its two sides, was relatively so modern an event, certainly subsequent to the origin of the more immediate ancestors of at least the arborescent members of the existing flora, it is certainly most misleading to talk of the perimeters of Patagonia as the places of origin of the Patagonian flora." It is probable that a desert area has for a long time been in existence in the area and therefore that the flora and its geological niche were in existence before they together occupied their present positions.

Entering Patagonia from the north one is immediately struck by the overall uniformity of the vegetation. Occasional clumps of pampas grass (*Cortaderia selloana* (Schult.) Aschers. & Graebn.) are reminders of the pampas flora being left behind but the shrub cover and sparse undercover immediately give the land its own character. The shrubs are tall in northern Patagonia but rapidly dwindle southward. They are predominantly either composits (*e.g., Baccharis marginalis* D. C., *Picris echinoides* L.) or Leguminosae (*e.g., Prosopis strombulifera* (Lam.) Benth.; *Cassia aphylla* Cav.), but there are also representatives of other families: *Atamisquea emarginata* Miers. (Capparidaceae), *Mulinum spinosum* (Cav.) Pers. (Umbelliferae) and *Montea aphylla* (Miers.) Gay (Scrophulariaceae). The common names of many of these (*e.g.,* algorrobilla, jarilla, mata negro) are in constant use by the natives and are found in much of the botanical literature.

The herbaceous layer abounds in composits, the white-flowered *Baccharis gilliesii* Gris., the yellow-flowered *Senecio pinnatus* Poir. and *Grindelia bergii* (Hieron.) Cabrera, or the wooly *Gnaphalium vira-vira* Molina. There are occasional cacti and many grasses such as *Polypogon elongatus* H. B. K., *Stipa papillosa* (Hack.) Hitchc., or *Pappophorum subbulbosum* Arech. The miscellaneous forbes represent many families, *e.g., Pfaffia* (Amaranthaceae), *Arjona* (Santalaceae), *Cryptantha globulifera* (Clos.) Reiche (Boraginaceae), *Verbena crithmithfolia* Gill. & Hook. (Verbenaceae), *Asclepias campestris* Dcne. (Asclepiadaceae) or *Sisymbrium* (Cruciferae). Entwined in the bushes where their weak stems gain support are species of *Mutisia* (Compositae) and *Caiophora* (Loasaceae).

Vegetationally the banks of the larger streams of Patagonia are disappointing. Rapidly eroding and subject to repeated inundations, they are not adapted to a stable plant cover. A patient search under tangled *Prosopis* bushes is necessary to find *Nothoscordum fragrans* Vent. (Liliaceae) or *Lilaea scilloides* Hauman (Scheuzeriaceae). Species of *Eleocharis* and *Scirpus,* well anchored with their deep root systems, are more common. *Picrosia longifolia* Don. (Compositae), *Senecio bergii* Hieron. (Compositae), *Satureia darwinii* (Benth.) Briq. and *Nicotiana* species (Solanaceae) may also be expected.

At the coast the land drops cliff-fashion into the sea, and the shore is said to be sinking. Sand dunes and salt marshes are rare. In a particularly favorable locality, perhaps at the mouth of one of the rivers, there might be found plants of familiar halophytic genera, such as *Spartina montevidensis* Arech. (Gramineae), *Salicornia peruviana* H. B. K. or *Suaeda divaricata* Moq. of the Chenopodiaceae, *Frankenia patagonica* Speg. or *Niederleinia juniperoides* Hieron. of the Frankeniaceae, or again *Senecio* (Compositae), *Cressa* (Convolvulaceae) or *Mesembryanthemum* (Aizoaceae). On the saline bottoms of the interior, occasional welcome breaks in the general monotony of the flora, one may expect to find, in addition, *Distichlis* (Gramineae), *Juncus* (Juncaceae) and perhaps *Chenopodium* (Chenopodiaceae).

Valleys where moisture is plentiful are comparatively rare. When springs occur they are usually surrounded by estancias and the vegetation is either much disturbed or heavily grazed. The

areas are dominated by sedges and rushes with occasional plantains, *Plantago juncoides* Lam or *P. barbata* Forst. var. *pauciflora* (Hook.) Pilger, (Plantaginaceae). The spots are brightened with the yellow-flowered *Mimulus glabratus* H. B. K. (Scrophulariaceae), the pink or purple of *Samolus* (Primulaceae) and the odd *Boopis filifolia* Speg. (Calyceraceae). If there is sufficient water to form a stream, the cold current is slowed by the stems and leaves of *Myriophyllum* (Halorrhagidaceae) or perhaps *Zannichellia palustris* L. (Potamogetonaceae).

In southern Patagonia the herbaceous growth is uniformly small in size and the shrubs are prostrate. The dwarf twisted growths of *Astragalus duseni* Macl. (Leguminosae), *Relbunium patagonicum* (Kuntze) Schum. (Rubiaceae), *Ephedra nana* Dusen (Gnetaceae) and *Nassauvia aculeata* Poepp. & Endl. (Compositae) are typical. In western Patagonia the shrubs thin out considerably and a grassland prairie formation forms a narrow transition between the Patagonian and Magellanic floras. Here the greatly increased and varied herbaceous layer may include *Alstroemeria patagonica* Phil. (Amarylidaceae), *Solenomelus sisyrinchium* (Gris.) Pax (Iridaceae), *Valeriana carnosa* Smith (Valerianaceae), *Jaborosa desiderata* Speg. (Solanaceae), *Aonikena patagonica* Speg. (Euphorbiaceae), *Colobanthus crassifolius* (D'Urv.) Hook. (Caryophyllaceae), *Psilocarphus chilensis* (Remy) Meigen (Compositae), *Plagiobotrys calandrinioides* (Ph.) Johnston (Boraginaceae), *Laretia acaulis* (Cav.) Hook. (Umbelliferae) and, perhaps most interesting of all, the tiny *Nicotiana acaulis* Speg. (Solanaceae) and the equally tiny *Calceolaria lanceolata* Cav. (Scropulariaceae) (40).

A picture of the botanical composition of some parts of Patagonia has been presented by Davies (14) who estimates *Festuca* sp. alone (including *F. ovina* var. *magellanica*) makes up to 65% of the ground cover in parts of southern Patagonia. Aside from the grasses the percentage of herbaceous plants in the total cover is seldom over 10%, and the woody plants, an extremely important part of the available forage, vary from practically absent to as high as 88%.

Quite naturally the first work on the flora of Patagonia was exploratory. In 1767–68 Philip Commerson, the botanist of Bougainville's French Exploring Expedition, made the first collections. He was followed by Anderson on Cook's Third Voyage, Menzies

(1796) on Vancouver's Voyage, and Charles Darwin (1831–1836) under Fitzroy on the Beagle. In 1839–43 J. D. Hooker as botanist under Captain Ross made very thorough collections. Then for the first time a collector returned to study his own material and publish the findings, the result being the "Flora antarctica" (26), the second volume of which includes the then known vegetation of southern South America. This early history is well summarized by Dusen (19, 20) who gives a list of all known expeditions to the region as well as a bibliography of the resultant works (see also 8, 46).

An early ecological description of the flora is given by Lorentz (34) who quotes a manuscript by Clarez and Heusser. One of the first theories concerning Patagonia was then already developed, first expressed by Darwin (13) and later by Ball (2). They suggested that the lack of trees in the area was due to the recent submergence of the land together with the absence of a neighboring forest to supply suitable trees. The pampas lie to the north and the mesophytic forest of the magellanic flora could hardly be expected to have quickly occupied the dry plains. Ball claims that this submergence is a more important contributing factor to the poverty of the flora than the harsh climate or the uniform sterility of the soil.

The poverty of the flora, undoubtedly a reflection of the uniformity of the habitat and the harshness of the climate, may be partly a reflection of the cramped space available for development. The tapered tip of South America is well flanked by broad bodies of water. In antarctic regions there are reported but two species of flowering plants, *Deschampsia antarctica* (Gramineae) and *Colobanthus crassifolius* (Caryophyllaceae), as opposed to over 400 in arctic regions (11). Present day antarctica must be ruled out at the start as a probable source of elements of the Patagonian flora, although, as will now be shown, the existence there of a temperate climate in the Tertiary has influenced the development of the flora of the region.

The idea of antarctic origins and dispersals has had many proponents, the first of which may well have been Hooker (27) who suggested that there were "many bonds of affinity between the three southern floras", these bonds being between Antarctica (southern South America and neighboring island groups), Australia and

Madagascar (South African links being more obscure) (22). Since then, many others (*e.g.*, 9, 42, 46, 49, 12), have given weight to the theory. Those who disagree maintain that the distributions represent isolated remnants of old northern floras (*e.g.*, 7). However, the flora of southern South America in which these links occur is not the xerophytic Patagonian flora but the hydrophytic flora best designated as the "Magellanic". This flora stands in its own right as distinct from the "Patagonian" flora discussed here. A possible exception to prove this rule may be found in the rare *Tetrachondra patagonica* Skottsb. (Tetrachondraceae), for the only other species of the genus occurs in New Zealand (47).

In spite of this denial of pan-antarctic elements in the Patagonian flora there is a secondary relationship through its endemic species. Nearly all these distinctive endemics which are found within the borders of Patagonia but not elsewhere have their immediate affinities with elements of the Magellanic flora. In general, these elements are species of moist swales. They are thus restricted in occurrence, this restriction being in many cases a consequence of the restriction of the habitat rather than a lack of aggressiveness on the part of the plant. In most cases they belong to genera whose names are unfamiliar to students of temperate floras of the northern hemisphere. Their development and distribution have been independent of the northern floras. Examples of plants in this category are:

Acaena macrostemon Hook. (Rosaceae)
Arjona tuberosa Cav. (Santalacaceae)
Boopis filifolia Speg. (Calyceraceae)
Carex subantarctica Speg. (Cyperaceae)
Chloraea magellanica Hook. f. (Orchidaceae)
Lepidophyllum cupressiforme Cav. (Compositae)
Lilaea subulata H. & Bonpl. (Lilaeaceae)
Scirpus cernuus Vahl (Cyperaceae)
Sisyrinchium humile Phil. (Iridaceae)
Verbena tridens Lag. (Verbenaceae)

Neither the foregoing list nor any of those which follow makes any attempt to be exhaustive. The few species listed are intended to be illustrative. Acknowledgment is here made of the great assistance received from I. M. Johnston's identifications on the plants

collected by the Univ. of California Second Botanical Garden Expedition to the Andes.

From a compilation of the literature Good (22) estimated the number of genera in the flora of temperate South America as 930, the number of species as about 12,250. It is questionable whether there is any floristic sense in his statement that "There is no marked demarkation between the flora of temperate South America and the floras of regions of the continent farther north", especially in light of his arbitrarily drawn borders. It is illogical to exclude Peru and Bolivia from a discussion of the temperate floras of South America.

According to Macloskie, Patagonia is dependent upon "a constant replenishing from the Andine (*sic*) chain and elevated valleys". Neger (39) also suggests the link, the river courses being the migration lanes. This link is the most natural of all, for not only are the migration lanes immediately apparent but there is greater similarity between the climates of these two areas than between any of the other adjoining areas. Low rainfall and cold winters are the dominant factors. This is the source of the largest proportion of the Patagonian flora. Characteristic species are the following:

Adesmia canescens (Gray) Benth. & Hook. (Leguminosae)
Alstroemeria patagonica Phil. (Liliaceae)
Anarthrophyllum rigidum (Gill.) Benth. & Hook. (Leguminosae)
Azorella caespitosa Cav. (Umbelliferae)
Berberis heterophylla Juss. (Berberidaceae)
Carex gayana Desv. (Cyperaceae)
Monnina angustifolia D. C. (Polygalaceae)
Quinchamalium majus Brogn. (Santalaceae)
Schinus dependens Ort. (Anacardiaceae)
Verbena mendocina Phil. (Cruciferae)

This continuity with the Andean chain opens the door to relationships with floras of other continents (23) which would otherwise be almost wholly lacking in the Patagonian flora. The effects of "transtropical highland bridges" on the distribution of temperate and even polar floras have been exhaustively treated by Du Rietz.

These species in most cases belong to genera for which a northern origin has been theorized, though in many cases a secondary center in temperate South America (often as well as in Africa and Australia) is evident. The following are characteristic genera:

Agrostis (Gramineae)
Alopecurus (Gramineae)
Anemone (Ranunculaceae)
Antennaria (Compositae)
Deschampsia (Gramineae)
Fragaria (Rosaceae)
Gentiana (Gentianaceae)
Geum (Rosaceae)
Luzula (Juncaceae)
Madia (Compositae)
Phleum (Gramineae)
Polemonium (Polemoniaceae)
Thalaspi (Cruciferae)
Viola (Violaceae)
Woodsia (Polypodiaceae)

Of longer standing than this present replenishing of the repeatedly inundated Patagonian plains is the floristic continuity between the desert regions of North and South America, first pointed out by Gray and Hooker (23), Engler (21), and Bray (9). Many of these species are halophytes. Johnston (29) has recently called attention to the conspecific character of many of the most typical shrubs of both regions. That this relationship may also be found in the herbaceous elements of the same floras has been shown by Beetle (4) for *Scirpus*.

Johnston (29) concludes that "we have every reason for believing in the past existence of a widely distributed desert flora. All the evidence indicates that, relatively isolated and free from competition, it has persisted in South America, while in North America, diluted by new xerophytes originating in the northern temperate lands, it has been giving way before their competition". Little convincing evidence has been offered as to how these temperate desert floral elements were able to bridge the tropics, whether carried by birds or mammals, or through dry inland basins. The following species have bicentric ranges, one part of their occurrence being in desert regions of South America and the other in desert regions of North America:

Atamisquea emarginata Miers. (Capparidaceae)
Koeberlinia spinosa Speg. (Capparidaceae)
Larrea divaricata Cav. (Zygophyllaceae)
Muhlenbergia asperifalio (Nees & Mey.) Parodi (Gramineae)
Scirpus nevadensis Wats. (Cyperaceae)

Lying immediately to the north, bordering Patagonia along the valley of the Rio Negro, is the flora of the pampas. Having a milder temperate climate with increased rainfall but without sharp barriers to southward migration, this area has contributed many species to the Patagonian flora. These species belong mostly to cosmopolitan genera and are frequently wide ranging. The Patagonian element is often separable as a variety rather than as a species, as in plants with affinities to the Magellanic flora. Presumably these rather aggressive types are rich in biotypes and consequently tolerant of a broad range of physical conditions (30, 50). Their spread into Patagonia is dependent on ecological specialization rather than chance dispersal from one ecological region to another:

Acaena pinnatifida R. & P. (Rosaceae)
Bromus catharticus Vahl (Gramineae)
Clematis montevidensis Spreng. (Ranunculaceae)
Eleocharis palustris (L.) R.Br. (Cyperaceae)
Glycyrrhiza astragalina Gill. (Leguminosae)
Lathyrus multiceps Clos. (Leguminosae)
Mimulus glabratus H. B. K. (Scropulariaceae)
Phacelia circinata Jacq. f. (Hydrophyllaceae)
Ranunculus bonariensis Poir. (Ranunculaceae)
Scirpus californicus (Mey.) Steud. (Cyperaceae)

Recent introductions, some of which are of economic importance for fuel and shelter, but which have no bearing on the historical phytogeography of the region, include the American willow (*Salix humboldtiana*) and the African tamarisk (*Tamarix gallica*). As in most inhabited corners of the world, a host of weeds of European origin are present. The earliest list of these species includes (5):

Brassica oleracea L. (Cruciferae)
Capsella bursa-pastoris (L.) Medic. (Cruciferae)
Cirsium arvense (L.) Scop. (Compositae)
Erodium cicutarium L'Herit. (Geraniaceae)
Hordeum murinum L. (Gramineae)
Portulaca oleracea L. (Portulacaceae)
Ranunculus repens L. (Ranunculaceae)
Sisymbrium officinale Scop. (Cruciferae)
Rumex crispus L. (Polygonaceae)
Taraxacum officinale Weber (Compositae)

SUMMARY

The Patagonian flora is mainly xerophytic in contrast to the hydrophytic Magellanic flora which borders it on the west. It is a complex of elements, each of which has originated from a different geographical region. The most unusual and peculiar endemics of Patagonia, for the most part plants of swales, have their closest relationships with the Magellanic flora. Most of the Patagonian species that belong to cosmopolitan genera are apparently derived from the pampus flora to the north. The largest part of the flora has its immediate affinities with the mountain flora of central Chile. The Patagonian species with a broad hiatus in range, usually halophytes, are related to elements of the desert flora of southwestern North America. To these groups may now be added the recently introduced weed flora which is largely from Europe.

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